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Hormonal Deficiency Causing Albinism in *Locusta migratoria*

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ABSTRACT—Hoppers of an albino strain in the migratory locust, *Locusta migratoria*, are uniformly creamy white when reared under crowded conditions. Implantation of corpora cardiaca taken from a normal hopper caused some albino hoppers to turn grey, reddish, brown, or dark brown like the colors of normal isolated solitary individuals, and others to develop the black and orange coloration like that of normal gregarious hoppers. Other organs such as brain and thoracic ganglia also induced various colors. Therefore, the albinism of this locust is caused by deficiency of some hormonal factor(s) present in the corpora cardiaca, brain and other ganglia. Implantation of some organs obtained from 7 other species also caused albino locusts to develop dark body colors, suggesting that some hormonal factor(s) commonly present in different insects can promote dark pigmentation in albino locusts.

INTRODUCTION

Genetic albinism appears to be caused by lack of the enzyme tyrosinase, which is required to produce the black pigment, melanin [6]. In the desert locust, *Schistocerca gregaria*, both enzyme and substrate for melanin formation are present, but melanization does not occur in albino individuals [10]. In the migratory locust, *Locusta migratoria*, the albino mutation is not uncommon and laboratory lines have been established to study the genetic and behavioral aspects of the albinism [5, 14, 21]. However, no information is available on the underlying mechanism causing this phenomenon. I present here evidence suggesting that albinism in *L. migratoria* is caused by deficiency of some hormonal factor(s) normally present in the brain, corpora cardiaca and thoracic ganglia of this species, and that a similar factor(s) inducing the dark coloration in albino locusts also exists in other insects including a katydid, crickets and moths.

MATERIALS AND METHODS

A colony of albino locusts of *L. migratoria* was maintained under crowded conditions at a 14 h (14L : 10D) photoperiod and 30°C since its establishment from albino individuals which appeared in a stock culture originating from Okinawa, Japan. The details of the rearing and handling methods have already been described [4, 20]. Various endocrine and nervous organs were removed from 1-day-old 5th instar hoppers, and transplanted with a small quantity of saline solution (3 μl; 0.9% NaCl) into 1-day-old 4th albino instars. A small incision was made between the 2nd and 3rd abdominal sternites of the recipients, and implants were injected into the body cavity using a micropipette. All hoppers were chilled on ice for 10–20 min before the operation and almost no mortality was observed in the recipients which were continusouly kept as groups. Four or 5 days after operation, they ecdysed to the 5th instar, and the body color of each individual was recorded 10 days after the operation. The same procedure was followed for transplantation of organs from other insects into albino locusts, and whether the recipients turned darker (+) or not (−) was recorded 10 days after operation. The donor species used included *Gryllus bimaculatus, Teleogryllus occipitalis, Modicogryllus confirmatus, Metriptera hime, Leucania separata, Bombyx mori,* and *Cephanodes hylas.*

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RESULTS AND DISCUSSION

When various endocrine organs and ganglia were taken from normal crowded hoppers, and transplanted into 4th-instar albino hoppers reared under crowded conditions, all implants except for suboesophageal ganglia (SG) promoted pigmentation in the albino hoppers (Table 1). However, the body color obtained was dependent upon the kind of organ implanted. Albinos implanted with a pair of corpora allata (CA) turned green (Fig. 1E). They looked like normal solitary hoppers except that the ventral side of their body remained whitish. This is consistent with the previous findings that implantation of extra CA or administration of juvenile hormone (JH) or JH analogues, to crowded hoppers induce the green solitary color [1, 2, 7, 8, 9, 15, 18, 19]. Implanted brains and thoracic ganglia induced various shades of grey, dark brown and straw yellow, the coloration being associated with normal non-green (="homochrome") solitary hoppers [16]. A similar color change was observed when albinos were implanted with CC, but in this case some developed the black patterns as well as the orange background color and became indistinguishable from the normal gregarious hoppers (Fig. 1 B, H). The black component of this gregarious coloration is attributed mostly to cuticular melanins [8, 16]. After

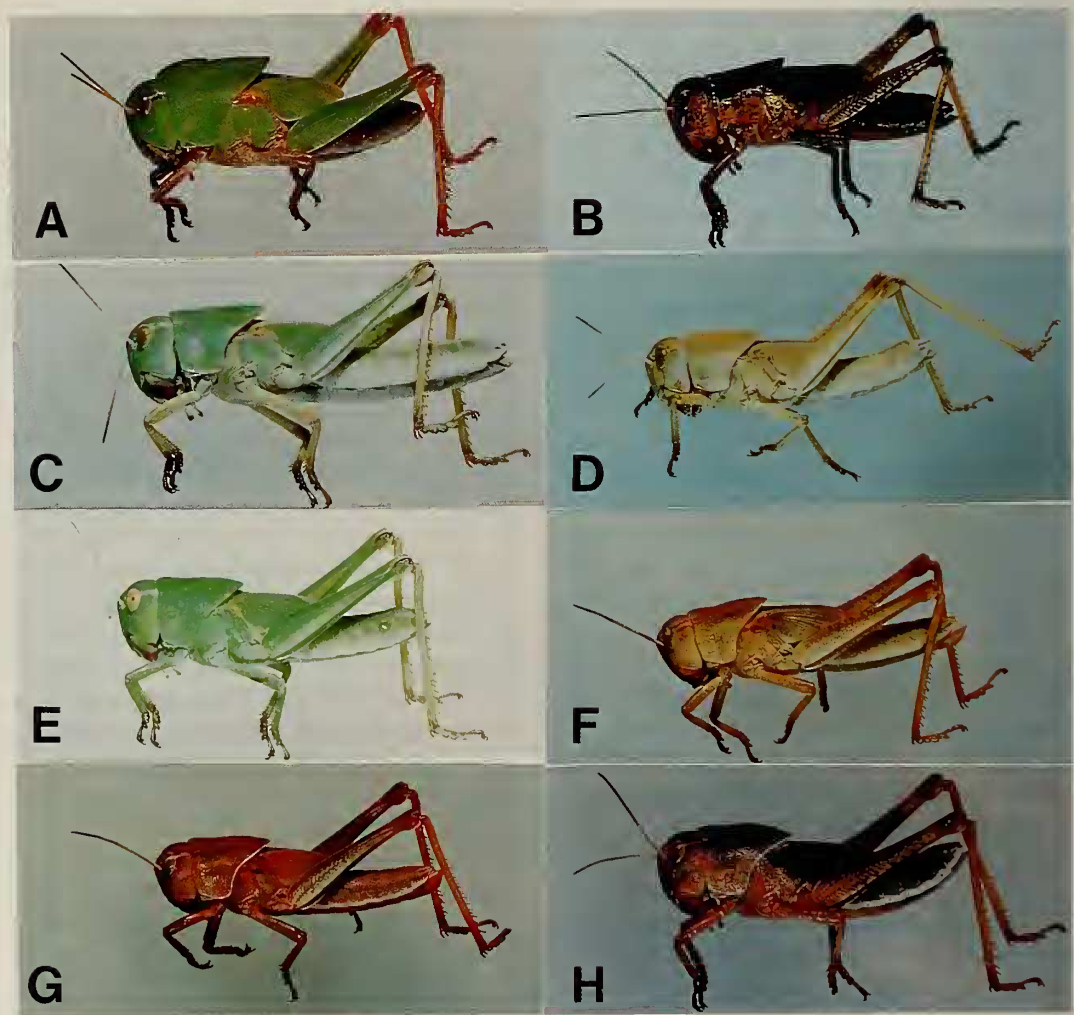

Fig. 1. Photographs of 5th instar hoppers of *L. migratoria*; normal solitary (A), normal crowded (gregarious)(B), albino isolated (C), albino crowded hopper without implantation (D) and albino crowded hoppers implanted with normal corpora allata (E), brains (F), or corpora cardiaca (G and H).

ecdysis, the melanins remain in the exuviae, while the pigments associated with the solitary form are mainly ommochromes, bile pigments and carotenoids [16] and do not remain in the exuviae. When a similar experiment was carried out with organs derived from field-collected green solitary hoppers, almost the same results were obtained ($\chi^2=1.37$; df=2; P>0.05; Table 1). This indicates that the factor promoting the gregarious black/orange coloration exists even in the CC of green solitary hoppers, although it either is not released or, if released, is inactive in the solitary

TABLE 1. Effects of implantation of various organs from 5th instar hoppers on the body color of albino hoppers in *L. migratoria*

Donors and Organs implanted	Color obtained in albino recipients: Solitary coloration				Greqarious coloration
	White	Green	Light homochromy	Dark homochromy	Black/orange
Normal (*Crowded in lab*)					
corpora allata (2)		10			
brain (1)			10	5	
corpora cardiaca (2)			3	7	5
thoracic ganglia (3)			9		
suboesophageal ganglia (3)	5				
Normal (*Field-collected solitary*)					
corpora cardiaca (2)			1	8	7
Albino (*Crowded in lab*)					
corpora allata (2)	1	9			
brains (1–2)	8				
corpora cardiaca (4–12)	15				
Albino (*Crowded in lab*)					
Control	20				

Donors were field-collected as 4th instars and reared individually in an outdoor insectary until used on the day after molting to the 5th instar. Numbers in the table indicate the numbers of individuals with the color indicated. Numbers in parentheses indicate the number of organs implanted. Controls included 10 intact crowded albino hoppers and 10 sham operated ones which were treated in the same way as the other operated hoppers except that no organ was implanted. Light homochromy includes straw yellow and brown, and dark homochromy reddish brown and dark brown.

TABLE 2. Effects of implantation of various organs from different insects on pigmentation in albino hoppers of *L. migratoria*

Donor species (Stage)	Organs impanted: Brain	Brain-SG	CC	SG
Gryllus bimaculatus (adult)	+		+	
Teleogryllus occipitalis (adult)	+		+	
Modicogryllus confirmatus (adult)	+		+	
Metriptera hime (larva)	+		+	
Leucania separata (larva)	+		+	–
Bombyx mori (pupa)		+		
Cephanodes hylas (larva)	+		+	–

The recipients either turned darker (+) or remained whitish (–) (N=3–10).

hoppers. By contrast, when CC or brains were taken from albino hoppers and implanted into other albino individuals, no color change occurred in the latter, although CA taken from albinos induced the green color (Table 1). From these results, it is concluded that genetic albinism in *L. migratoria* is due to a deficiency of some hormonal factors normally present in the CC, brain and other nervous ganglia.

The brown or black coloration could also be induced in albino hoppers by implantation of CC, brain or other nervous organs from other insects (Table 2). Melanization in the common armyworm, *L. separata,* is known to be induced by a hormone (the melanization and reddish coloration hormone) secreted from the brain-CC-CA complex or the SG [11, 17]. Albino hoppers developed brown pigments when implanted with a brain-CC complex from the armyworm, but no pigmentation was elicited by implantation of even 6 SG. In the cricket, *G. bimaculatus,* melanization is suppressed by the juvenile hormone produced by the CA, but the factor causing melanization has not been identified [2]. Implantation of CA from three species of crickets into albino locusts turned the recipients green (data not shown) while that of CC induced strong melanization in the albino locusts (Table 2). These results suggest that some hormonal factor(s) commonly present in different insects can promote dark pigmentation in albino locusts.

In this study, the gregarious coloration was obtained only in those albinos which had been implanted with CC from normal locusts, but whether the factor responsible for this coloration occurs only in CC or not remains uncertain. The involvement of CC and brain in the induction of dark pigments has been suggested using normal individuals of *L. migratoria* [3, 12, 13]. But, the substance(s) leading to the expression of the gregarious black color and/or the solitary black homochromy has not been identified chemically. The major obstacles to such a study include (i) difficulty in obtaining a large number of solitary hoppers for a bioassay and (ii) inability to remove the underlying background color or homochromy from such solitary individuals. The albino strain may provide an excellent bioassay system for endocrinological studies on phase polychromism in locusts.

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